NASA TT F-11,284

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Translation of "Sauerstoffaufnahme und respiratorische Funktionen in grossen Hoehen". Skandinavisches Archiv fuer Physiologie, Berlin, Vol 76, 1937, pages 88-100.

NATIONAL AERONAUTICS AND SPACE ADMINISTRATION
WASHINGTON DECEMBER 1967

OXYGEN CONSUMPTION AND RESPIRATORY FUNCTIONS AT HIGH ALTITUDES[1]

Skandinavisches Archiv Fur Physiologie (Scandinavian Record of Physiology), Berlin, Vol 76 1937: 88-100

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The contemporary concept of mountain sickness is that it is definitely not a "metabolic disease". The symptoms of the disease are not explained by the accumulation of incompletely oxidized metabolic products in the body. Even at high altitudes, under normal conditions, at rest, as a rule, tissues receive a sufficient amount of oxygen. Whenever clear symptoms of lack of O_2 appear, they were probably caused by the central nervous system, when confronted by too low a pressure of oxygen. <u>The body not only requires a sufficient amount of oxygen, but also a sufficiently high pressure of the arterial blood</u>.

Tissues can be adequately supplied with sufficient amounts of O_2 when the respiratory and circulatory systems work well together. Of course, the supply of adequate O_2- tension depends on the O_2- tension of the inhaled air, but mostly on the efficiency of the respiratory system (Christensen and Krogh, 1936). A drop in alveolar O_2- tension can be effectively

(1) Manuscript submitted 12 January 1937

(2) Supported by the Carlsberg and Rask-Orsted Funds and by the Rockefeller Foundation

counteracted by increased ventilation of the lungs. From the following experimental results, it will become clear how extraordinarily large respiratory requirements can become at high altitudes.

Plan of the Experiment and Methods

The experiments were performed in the morning before eating. The work machine was the Fahrradergometer, already described (Christensen and Forbes, 1937) which permitted large changes in work intensity. The simple Ergometer gave sufficiently precise measurements, as indicated by control measurements with Krogh's Fahrradergometer, which could be braked electro-magnetically. Most of the metabolic determinations were done by the method of Douglas. In some experiments, the exhaled air was collected directly in a large Spirometer. The accuracy of the measurements of metabolic changes was not as good as that obtained under normal experimental conditions. The largest source of error was the fluctuation of the temperature of the experimental room. At stations Chuquicamata (2810 m), Ollague (3660 m) and Collahuasi (4700 m), the experimental room was a railroad car converted into a laboratory. At Aucanquilcha (5340 m), the experiments were performed in a house. There, too, the temperature fluctuated much. During the morning, the temperature of the interior of the railroad car rose from 10^{o} to $30^{o}C$. This change of the temperature of the air interfered with the measurement of the volume of exhaled air. The precision of the analysis was less affected, because the analytical apparatus - Haldane's apparatus modified by Krogh - was placed in a well-insulated room.

The relatively small dispersion of the experimental data indicated that the precision of the measurements sufficed for the task on hand.

From subjects at rest, samples of alveolar air were collected in a small rubber bag having a capacity of 3-4 liters. Breathing was done freely through a three-way stopcock, open to the atmosphere. After a normal exhalation, the director of the experiment gave a command, and a deep and rapidly exhaled sample was produced for the usual Haldane test. At the same time, the director turns the stopcock such that the exhaled air is collected in the rubber bag. The small and empty space of the bag was thoroughly flushed with alveolar air prior to the experiment. The samples of alveolar air corresponded to the exhaled alveolar air samples of Haldane and Priestley, i.e. the observed CO_2-tension was slightly above and the O_2-tension was slightly below the average alveolar tension. This method is very useful for subjects who were quickly trained. During the experiments, samples of alveolar air were removed as refractive samples from the exhalation side of the respiratory valve.

Oxygen Intake During Muscular Work

A correlation between work-intensity and total O_2-intake for subject EHC at different altitudes is shown in Figure 1.

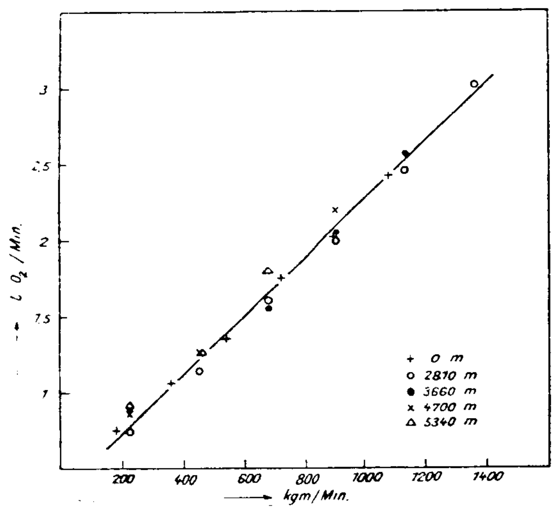

Fig. 1. O_2-intake and work intensity of subject EHC

At the termination of the expedition, values were obtained during work on Krogh's Ergometer at sealevel. The other values were obtained within a two months period, usually after a few days of stay at a given altitude. The values are probably not much influenced by variable conditions of training, because the subjects were trained on the Fahrradergometer before the start of an experiment. Oxygen-intake increased as a straight line when plotted against work-intensity at all altitudes between 0 and 5300 m. At different altitudes, the intake of O_2/kgm of work was the same. Measurements on other subjects showed that, in general, useful work was independent of altitude. At high altitudes, in some cases, the O_2-intake per kgm of work was insignificantly higher than the average value. This may have been caused by an increased amount of breathing (Nielsen, 1936).

In Figure 2 there are shown the curve of Figure 1 and corresponding curves obtained from four other members of the expedition. The shape of the curves indicates that in all five subjects there existed the same correlation between O_2-intake and work-intensity at different altitudes. The individual differences were very small.

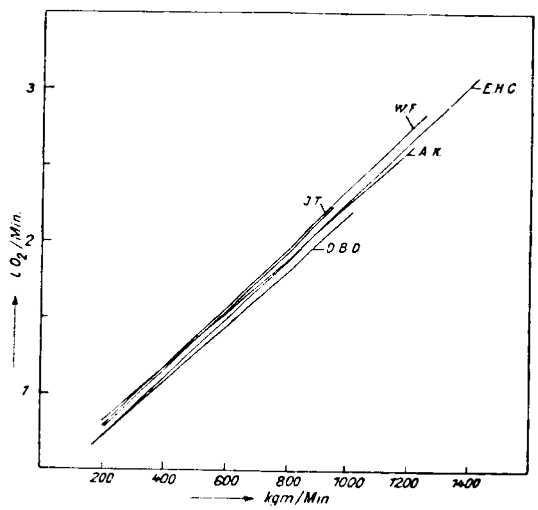

Fig. 2. O_2-intake and Work-intensity

The results were in good agreement with the data of Dill and associates (1931), who performed work experiments with a Fahrradergometer at an altitude of 3100 m. The unimportant, but improved useful work at the higher altitude, found in our experiments, may be ascribed to better training.

Older publications did not explain, for certain, the degree of efficiency of muscular work at different altitudes.

For example, the very carefully obtained data of Haldane et al. (1912) on top of Pike's Peak indicated how extraordinarily difficult a comparison can be between walking-work at sealevel and a high altitude. The type of construction of the walking-train has a decisive influence on the economy of walking (Durig et al., 1909). Work on a Fahrradergometer is to be preferred, because the work output can be kept constant at every altitude and this enables one to make strict comparisons.

As a rule, older investigators found decreased useful work at higher altitudes. On the contrary, Haldane et al., using an excellent walking-train on Pike's Peak, found increased useful work.

Herxheimer et al (1933) claimed that metabolic measurements made only during the work-period did not provide definite information about the metabolic economy of work. This may have been in error. These authors observed very large individual variations in efficiency of work, undoubtedly caused by an unsuitable experimental technique, indicated by the large deviations of the data.

With respect to the degree of efficiency, we have only considered the direct consumption of O_2. We did not calculate the caloric value of O_2 at the observed respiratory quotient. As a rule, metabolic measurements were made 8-10 minutes after the start of the work. Since CO_2-washings were not always completed by then, the R.Q. does not indicate clearly the state of the metabolism. However, the observed R.Q. values indicated that carbohydrates were more strongly oxidized at higher altitudes.

Ventilation

Ventilation, designated as V_{37} (37^o existing pressure and vapor saturation), increased strongly with falling barometric pressure for equal amounts of O_2-intake. In Figure 3, results are presented which were produced by subject EHC. Others gave similar results, but fewer determinations were made. In Figure 3, V_{37} is shown in relation to O_2-intake.

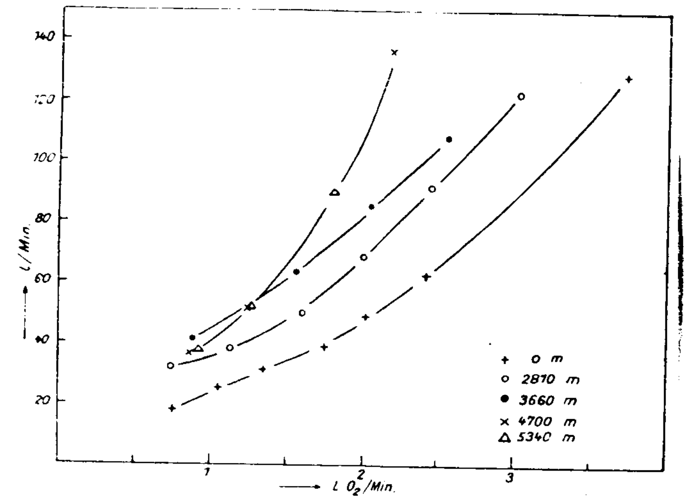

Fig. 3. V_{37} and O_2-intake by subject EHC

Values at sealevel were obtained last, as mentioned earlier. They showed a normal value for V_{37} at different O_2-intakes, i.e. about 25 liters per liter of consumed O_2. The form of the curve indicates that V_{37} is relatively larger with the largest O_2-intake than it is with the smaller O_2-intakes. The same form of the curve is found again at different altitudes, but there is a much stronger increase accompanying the largest O_2-intake. Table 1 shows values of curves for V_{37} for an O_2-intake of 2 liters/minute.

Table 1

Altitude in m	0	2810	3660	4700
V_{37} 2 liter O_2/min	48	69	83	110

This table shows a strong increase in V37 during a decrease in total pressure. If the value of V_{37} would have been the same for oxygen at all altitudes, then the inhaled amount of O_2 would have decreased proportionately with the barometric pressure. The consequences of decreasing barometric pressure are compensated for by a larger V_{37}. As is shown in Figure 4, this compensation is extraordinarily effective.

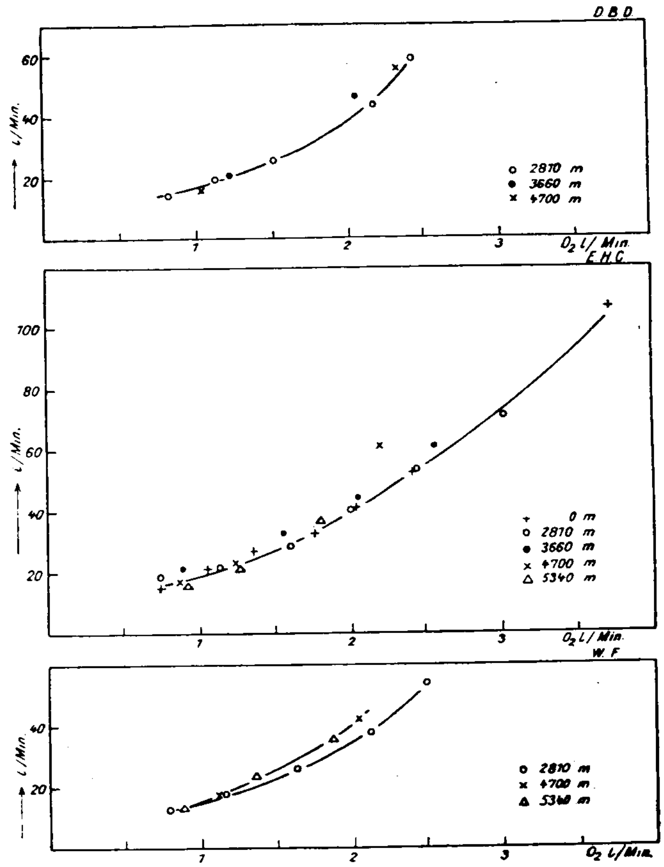

Fig. 4. V_0 and O_2-intake for subjects DBD, EHC and WF

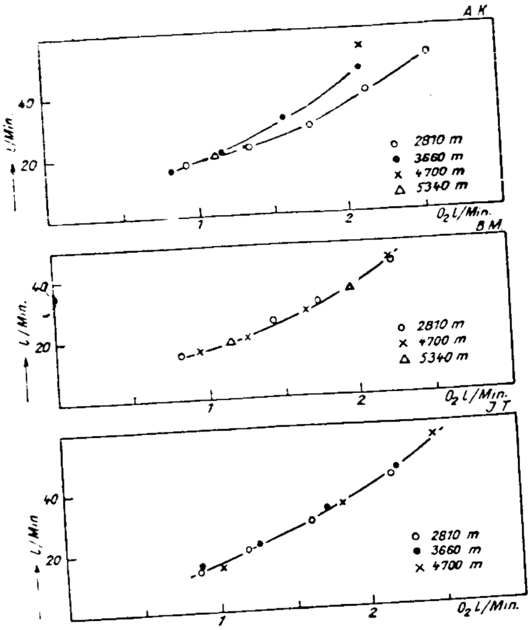

Fig. 4 continued. V_0 and O_2-intake of subjects AK, BM and JT

Figure 4 indicates that V_0 (volume of respiration 0^o, 760 mm Hg, dry) for a given O_2-intake is almost constant at all altitudes and that the amount of O_2-inhaled per minute, at a given metabolism, is almost unchanged at all heights. Two subjects showed a slight, but unmistakable increase in V_0 with increasing altitude. During maximum O_2-intake, when the subjects were driven to the limits of their work-ability and when they were psychologically excited (upset), values were often obtained for V_0 which fell outside the normal range. These high values are best explained by assuming an over-stimulation of the respiratory center. For example, subject EHC showed an O_2-intake of 2.2 liters/minute at an altitude of 4700 m with a V_{37} of not less than 136 liters/minute and a corresponding V_0 of 61 liters/minute. This V_0 value fell outside the normal range, as shown in Figure 4.

Alveolar Air

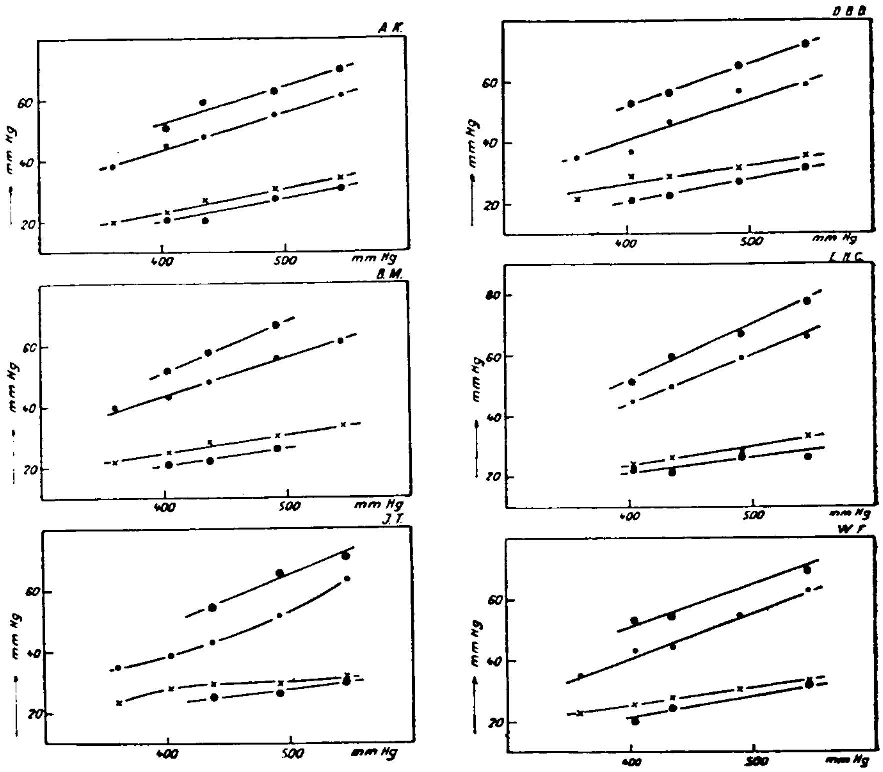

Fig. 5. Alveolar tension and barometric pressure of subjects AK, BM, JT, DBD, EHC and WF at rest and work

In figure 5 there are shown alveolar O_2 and CO_2 tensions at rest and at work (muscular activity) at altitudes between 2810 m (543 mm) and 5340 m (401 mm), as well as single determinations at rest at an altitude of 6140 m (356 mm). Averages of numerous single determinations were calculated. The values obtained during work are the averages of all work-values at a given altitude. Work-intensity was not considered. All the subjects, except subject JT, showed a straight-line decrease of alveolar air and CO_2-tension at rest and at work (muscular activity). In all cases, the values for alveolar O_2 were higher and the corresponding CO_2-tension per 100 mm Hg drop in total pressure, expressed as an average of all subjects, was 6.5 mm at rest and 6.3 mm at work. The corresponding values for a drop in O_2-tension were 13.7 mm at rest and 15.1 mm at work (muscular activity).

Earlier reports by Fitzgerald (1913) and Hasselbalch and Lindhard (1915) also indicated a straight-line decrease in tension with decreasing barometric pressure. The CO_2-tensions reported by Fitzgerald showed a decrease of 4.2 mm Hg per 100 mm Hg drop in barometric pressure, while the corresponding value reported by Hasselbalch and Lindhard was 3.8 mm Hg.

Table 2

Observed and Calculated Alveolar Tensions at Rest

Vp.	1 Druck 550 mm Hg	2 Druck 400 mm Hg		3 Druck 550 mm Hg	4 Druck 400 mm Hg	
	5 CO_2-Spann. mm Hg	6 gefundene CO_2-Spann. mm Hg	7 berechnete CO_2-Spann. mm Hg	O_2-Spann. mm Hg	9 gefundene O_2-Spann. mm Hg	10 berechnete O_2-Spann. mm Hg
EHC	33.2	23.8	23.3	68.0	44.0	47.8
DBD	35.1	26.3	24.6	61.0	40.9	42.8
HTE	34.0	22.8	23.9	62.8	43.3	44.1
W. F.	33.5	25.0	23.5	62.8	40.3	44.1
A. K.	34.7	23.0	24.3	62.0	43.5	43.5
B. M.	33.3	24.7	23.4	62.0	43.1	43.5
Durchschnitt	34.0	24.3	23.8	63.1	42.5	44.3

Table 3

Observed and Calculated Alveolar Tensions at Work (Muscular Activity)

EHC	29.0	21.2	20.4	79.0	52.2	55.4
DBD	32.1	20.6	22.5	73.1	52.0	51.3
W. F.	31.2	21.2	21.9	72.0	51.0	50.5
A. K.	31.8	20.3	22.3	70.3	52.3	49.5
B. M.	29.0	20.6	20.4	75.9	50.9	53.3
J. T.	30.0	23.0	21.1	73.0	48.9	51.2
Durchschnitt	30.5	21.2	21.4	73.9	51.2	51.9

(Headings on next page)

(Headings for Table 3)

Vp. = subjects
1 = pressure 550 mm Hg
2 = pressure 400 mm Hg
3 = pressure 550 mm Hg
4 = pressure 400 mm Hg
5 = CO_2-tension mm Hg
6 = obs. CO_2-tension
7 = calc. CO_2-tension
8 = O_2-tension mm Hg
9 = obs. O_2-tension
10 = calc. O_2-tension

Tables 2 and 3 were compiled in order to investigate the magnitude of the decrease in CO_2 and O_2-tensions of alveolar air in relation to decreasing barometric pressure. Values of the curves for observed tensions at barometric pressures of 550 and 400 mm Hg were tabulated. Also, the CO_2 and O_2-tensions at 400 mm Hg were calculated on the assumption that they decreased proportionally with barometric pressure. Tables 2 and 3 show that, as a rule, there is good agreement between the observed and calculated tensions. In the subjects tested and at the stated altitudes, alveolar CO_2 and O_2-tensions fell nearly proportionally with decreasing barometric pressure. The percentage of alveolar CO_2 and O_2 was almost constant. This leads to the conclusion that alveolar ventilation was nearly equal at 0° and per liter of O_2, at rest and at work, at different altitudes. This is in good agreement with the reduced total ventilation per liter of O_2 during muscular activity which was almost equal at different altitudes.

Discussion

The experimental results discussed above indicated, among other things, that O_2-intake per kgm of muscular activity was almost equal at all altitudes investigated. When the maximum O_2-intake was compared at different altitudes, a definite dependence on altitude was observed and this was expected. In Table 4, below, we show the maximum O_2-intake for subject EHC, who provided the most complete set of data, at different altitudes, with respect to ventilation, alveolar gas tension and pulse frequency.

Table 4 shows that maximum O_2-intake and, therefore, maximum ability to do work, decreased strongly with decreasing barometric pressures. At an altitude of 0 m, the maximum ability to do work was 1500-1600 kgm/min with an O_2-intake of 3.7 liters/min. At an altitude of 4700 m, the respective values were 910 kgm/min and 2.2 l O_2/min. At an altitude of 5340 m, maximum ability to do work had decreased to 680 kgm/min and the maximum O_2-intake had decreased to 1.8 l O_2/min. At that altitude, the general condition of subject EHC was not good, because of fatigue and insomnia.

Table 4

Maximum Ability to Do Work of Subject EHC

Höhe m Bar. mm. Hg. 1	0 m 760 mm	2810 543 mm	3660 480 mm	4700 429 mm	5340 401 mm
Max. O_2-Aufnahme Liter pro Min. 2	3.72	3.02	2.56	2.19	1.80
Ventil. Liter/Min. 37° vorh. Druck. Dampfsätt. 3	120.1	122.0	108.3	136.1	89.5
Ventil. Liter/Min. 0° 760 mm trocken 4	106.7	71.2	61.3	61.1	36.8
Alveol. O_2-Spannung mm. Hg. 5	124.0[1])	80.6	71.2	61.8	53.3
Alveol. CO_2-Spannung mm. Hg. 6	26.0[1])	25.3	26.6	19.9	20.7
Pulsfrequenz bei max. O_2-Aufnahme 7	190	170	150	135	132

(1) Exhaled air; at this large ventilation, the tension of the exhaled air deviated but little from the alveolar tension

Headings:
1 = altitude in m
pressure mm Hg
2 = maximum O_2-intake l/min
3 = ventilation l/min
37° existing pressure
saturated vapor
4 = ventilation l/min
0°, 760 mm Hg, dry
5 = alveolar O_2-tension mm Hg
6 = alveolar CO_2-tension mm Hg
7 = pulse frequency at maximum O_2-intake

Also shown in Table 4 is the fact that although the maximum O_2-intake decreases strongly with increasing altitude,

V_{37} is very near the maximum limit at all altitudes, except the highest where, perhaps, special factors become operative. V_{37} is a measure of the burden of the respiratory system. When V_{37} at a barometric pressure of 429 mm Hg and a maximum O_2-intake of 2.2 l/min is compared with the corresponding value at normal pressure, it may be seen that V_{37} rose from 54 liters (see Fig. 3) to 136 liters; an increase of 150%. An additional increase in V_{37} is not conceivable. Simultaneously, the corresponding frequency of the pulse indicated that the circulation was not burdened to the maximum at maximum O_2-intake at different altitudes. At 429 mm Hg, the pulse frequency was 130-135/min, the maximum O_2-intake was 2.2 liters. At sealevel, the pulse frequency had the same value when the same amount of O_2 was taken in.

Christensen and Forbes (1937) reported that in persons with a healthy circulation, the circulatory system is not particularly burdened at higher altitudes. Circulation does not become the limiting factor for possible O_2-intake under such conditions. The reported values for V_{37} under maximum O_2-intake, at different altitudes, make it appear that ventilation is the limiting factor for respiratory metabolism and, consequently, for the ability to do work at high altitudes. The relatively low alveolar O_2-values found at high altitudes indicate that a steep decrease of alveolar O_2-tension could not be avoided despite enormous ventilation.

Even at rest, breathing can be of decisive importance for the ability to tolerate low O_2-tension in inhaled air. For example, Christensen and Krogh (1936) demonstrated that among 50 high-altitude pilots there existed a close relationship between tolerance against low O_2-tension in the inhaled air and increased ventilation. Only those subjects who showed a definite increase in ventilation were able to tolerate very low O_2-tensions. During muscular activity, when O_2-intake is markedly increased, it becomes of decisive importance that the alveolar O_2-tension remain high, thereby favoring the diffusion of O_2. Without exception, the observed values indicated higher alveolar O_2-tensions at rest and at work.

The results reported here indicated unmistakably that the ability to do work over extended periods at high altitudes decreased strongly. This was not true for short-term work.

Christensen and Nielsen (1936) reported that muscle strength was unchanged at high altitudes. This was probably related to the fact that the O_2-supply of working muscles during the work-period, when short times were used, had no effect on muscle efficiency (see Herxheimer, 1933).

Summary

A study was made of the effect of high altitudes on oxygen intake during muscular activity and on respiration during rest and work. The results indicated that during work ~~on the Fahrradergometer~~ all subjects showed the same relationship between work intensity and O_2-intake at different altitudes. The degree of efficiency was not affected by the altitude. Lung ventilation, V_{37}, was not reduced and increased strongly with increasing altitude, reaching a value of more than 120 liters/minute during work.

Reduced lung ventilation V_0 was constant at identical O_2-intake at all altitudes investigated. At all heights, the alveolar O_2-tension was higher at work than at rest. At high altitudes, the maximum oxygen intake was limited by the ventilation of the lungs.

The experimental data for this report were taken from "The International High Altitude Expedition to Chile" (1935). The expedition was supported by the Fatigue Laboratory and the Milton Fund, Harvard University, University of Copenhagen, Carlsberg and Rask-Orsted Funds, Copenhagen, King's College, Cambridge University, Corn Industries Research Foundation, Columbia University, National Research Council, Royal Society of London, Josial Macy Foundation, American Association for the Advancement of Science, and numerous institutions in Chile.

Literature